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MAINTENANCE OF CONSTANT LEAF TEMPERATURE BY PLANTS—I. HYPOTHESIS—LIMITED HOMEOTHERMY

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MAHAN J. R. and UPCHURCH D. R. *Maintenance of constant leaf temperature by plants—I. Hypothesis—limited homeothermy*. ENVIRONMENTAL AND EXPERIMENTAL BOTANY **28,** 351–357, 1988.—The relationship between the temperature of a plant and the temperature of its environment is an important consideration in the study of thermal stress. Plants are generally assumed to be poikilotherms that exist in eurythermal environments and some variation in plant temperature is thought to be normal for the plant. Recent investigations in our laboratory have indicated that the thermal dependencies of enzymes from several plants are more characteristic of those from homeotherms than eurytherms. Thus, while it is assumed that thermal variation is normal for a plant, the thermal dependencies of the enzymes of the plant suggest that such variation may be stressful. We present a conceptual framework for the active maintenance of a normative, or characteristic, temperature by the plant. We propose that the lower limit of the temperature of a plant is controlled by its environment while the upper limit, even under a wide variety of conditions, can be controlled by the plant and maintained at a normative value. We suggest the term "limited homeothermy" to describe this type of thermal behavior by the plant. We propose three constraints on the maintenance of the normative temperature by the plant; (1) sufficient energy influx to raise its temperature to the normative value, (2) sufficient water supply for transpiration, and (3) humidity low enough to allow for cooling to the normative temperature.

INTRODUCTION

PLANTS grown worldwide are exposed to seasonal and diurnal variations in temperature. This variation often results in temperature stresses that limit the feasibility and profitability of cultivation of certain plants. Effects of temperature on plants are of major importance and thus have been the object of many investigations which have been well reviewed.[3,7,12]

The effect of thermal variation on plants is dependent upon the degree of variation that is normal for the plant. The specific range of temperatures that are non-stressful for a given plant is often difficult to determine. Plants are generally described as poikilotherms.[7,9] Poikilotherms are organisms whose temperature is determined entirely by their environment. Some poikilotherms (e.g. fish and reptiles) are able to limit variation in their body temperature by moving to more favorable environments when necessary. The immobile nature of plants and the fact that they frequently are found in environments that are subject to wide variations in temperature (i.e. eurythermal) have resulted in the assumption that plants are eurythermal poikilotherms and led at least one author to describe them as the "epitome of poikilothermy".[9]

Radiometrically determined canopy temperatures have been used extensively in the prediction of evapotranspiration. The evaporation of water is an endothermic process and will often cause the temperature of a plant canopy to be less than the ambient air temperature. The relationship between the temperature of a plant canopy as determined by a radiometer and the temperature of the air above the canopy has been used as a measure of crop water stress.[6,14] The theoretical relationship described by JACKSON *et al.*[6] assumes that the temperature of a plant canopy is not a constant. Even with optimal water availability, canopy temperature will vary with ambient microclimate factors. The temperature of a plant canopy is determined by the balance between energy gains and energy loss. The physical characteristics of the interaction of the plant with its environment have been developed and explained in great detail by CAMPBELL[2] who has stated that the leaf temperature is not directly controlled by the plant but rather by the rate of receipt, loss and storage of energy by the leaf.

The ability of various organisms to exist in highly diverse thermal environments has led to the study of the mechanisms and adaptations that allow the organisms to survive, and in many cases flourish, in potentially harsh environments. There has been particular interest in the means by which enzymes (which are, in general, highly temperature dependent) are able to function effectively at different temperatures. The apparent Michaelis constant (K_m) of an enzyme for a substrate is the concentration of substrate required for the reaction velocity to reach one half of the maximum rate (V_{max}). The rate of an enzyme reaction is dependent upon the value of the K_m and the cellular substrate concentration. The K_ms of enzymes are known to be dependent on temperature and therefore present a possible mechanism for temperature to affect enzyme reactions. Various organisms that have evolved for life in different thermal environments have enzymes that, while often similar in many other respects, are adapted for optimal function at unique temperatures. SOMERO and LOW[11] reported the thermal dependence of the function of the enzyme pyruvate kinase from stenothermal and eurythermal species of fish that live in different thermal environments. They found that the thermal region of minimal K_m values corresponded with the normative temperature of the species. In a fish from a variable thermal environment, the optimal function of the enzyme occurred over the wide thermal range 10–30°C that was normative for that fish. The optimal function of the enzyme from two species of fish which were endemic to relatively constant thermal environments of −2°C and 40°C, occurred at temperatures below 5°C and above 30°C, respectively. Thus the enzymes from eurytherms were found to function optimally over a wide range of temperatures while enzymes from stenotherms were limited to optimal function over thermal ranges that are characteristically narrow (Fig. 1A). Enzymes from different stenotherms can be limited to optimal function over unique thermal ranges (Fig. 1B).

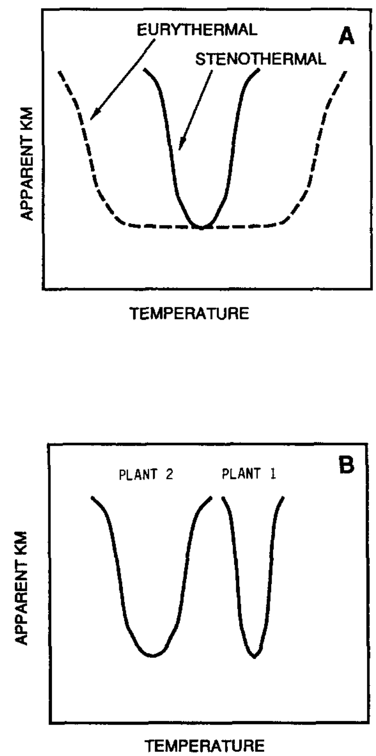

FIG. 1. Thermal dependencies representative of various types of organisms. (A) Eurythermal and stenothermal. (B) Stenothermal enzymes with different optimal ranges.

We have reported the thermal dependence of the apparent K_m of two enzymes from several plant species as part of our effort to define the thermal limits of optimal function for the enzymes and by extension the metabolism of the plant.[1,8] We have found that the apparent K_m is: (1) highly temperature dependent and (2) that the thermal dependencies are species specific. The thermal dependencies are uncharacteristically narrow for enzymes from organisms that experience variable thermal environments. These narrow thermal ranges of optimal function are commonly found in organisms from stable thermal environments. This finding is paradoxical in that plants are often subject to highly variable thermal environments yet, as poikilotherms, supposedly have no biological mechanisms for maintaining a specific temperature, and suggests that plant enzymes may be routinely subject to thermal limitations. Such a chronic thermal limitation of the function of enzymes would impact the metabolism of the plant and could limit the function of the whole plant.

The fact that we find apparently stenothermal enzymes in plants that are assumed to be highly eurythermal has led us to question whether plants may indeed have some biological mechanism for controlling their temperature. If the plant could control its leaf temperature, we predict that there would be a normative temperature that would be preferentially maintained by the plant. This normative plant temperature (T_n) would be an inherent characteristic of the plant. The maintenance of leaf temperature at the T_n would allow the plant to carry out its metabolic functions at a stable temperature in spite of thermal variation in its environment.

MECHANISMS

Maintenance of a specific temperature within a variable thermal environment requires the ability to balance the energy fluxes into and out of its leaves (Fig. 2) as well as a biological thermal sensing mechanism.

The plant has two primary mechanisms for balancing energy effluxes to its environment (Block B); the liberation of chemical energy through respiration (Block E) and increasing the amount of energy absorbed from the atmosphere (Block D). While many organisms rely upon the liberation of energy through respiration to offset energy effluxes to the environment the respiratory systems of plant cells are not large enough to produce sufficient heat to offset energy losses.[7,10] Changes in the position of leaves can increase the interception of radiant energy. Leaf movements can modulate the energy balance (and thereby temperature) of the leaf substantially. Thus the plant is limited in its ability to compensate for losses of energy to its environment and with the exception of positive heliotropic behavior, has little or no control over the lower limit of its temperature.

The plant has four mechanisms for balancing influxes from its environment (Block C). Negative heliotropism and wilting (Block F) are mechanisms which allow the plant to reduce the amount of radiant energy absorbed from the environment. The plant can also dissipate energy through the processes of convection and reradiation (Blocks G and H). The evaporation of water from the leaf can dissipate large amounts of incoming energy (Block I) and depressions in leaf temperature on the order of 10–15°C below air temperature by transpiration are theoretically possible.[6]

HYPOTHESIS—LIMITED HOMEOTHERMY

The preceding section establishes that plants have substantial mechanisms for offsetting energy influxes but have limited mechanisms for offsetting energy effluxes. In simple terms this means that the plant has powerful means for reducing its temperature but very limited means for increasing it. The existence of a biological thermal sensor/controller of transpiration might allow the plant to function as a limited homeotherm. The temperature of a limited homeotherm would be dictated by the environment when its temperature is below a normative temperature but when energy influxes are sufficient it would be capable of maintaining a normative temperature. Within a wide variety of defined environments the temperature of the plant acting as a limited homeotherm would be relatively constant.

In accord with our hypothesis of limited homeothermy there are three environmental limitations on the maintenance of constant leaf temperature by plants: (1) sufficient energy influx to raise its temperature to the normative value, (2) sufficient water supply for transpiration, and (3) humidity low enough to provide for

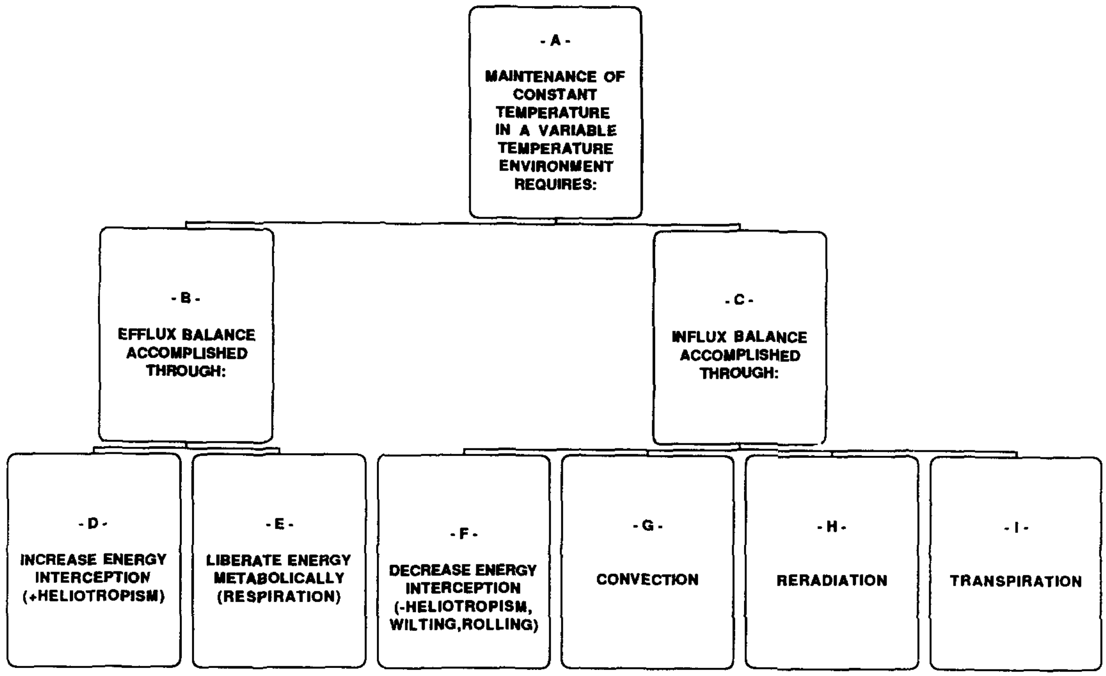

FIG. 2. Diagram of some mechanisms used by organisms to limit thermal variation.

cooling to the normative temperature. Figure 3 is a hypothetical comparison of the temperatures of two limited homeotherms that have different T_ns (see Fig. 1B) with the temperature of the surrounding air over a diurnal cycle. The three proposed environmental limitations are demonstrated and will be discussed in the following section.

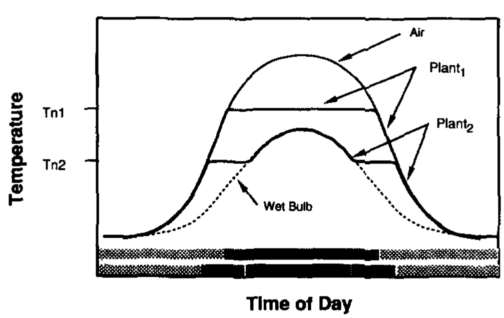

FIG. 3. Hypothetical comparison of air temperature with the temperatures of two limited homeotherms that have different normative temperatures. The normative temperature of plant 1 is greater than that of plant 2. Homeothermic behavior (■), and non-homeothermic behavior due to (1) insufficient energy influx (▨) and (2) humidity (▩) are demonstrated.

Sufficient energy input

Homeothermic behavior in plants will be limited to conditions under which the energy influx (sensible heat or radiant energy) is sufficient to raise the leaf temperature to the T_n. This constraint results from the limited ability of the plant to balance energy effluxes to its environment (i.e. its limited ability to warm itself). In those instances where energy is limiting, the plant is essentially a poikilotherm and as such its temperature will be determined by, but not necessarily equal to, that of the surrounding environment. When energy inputs to the leaf are sufficient to raise its temperature to or above the normative value, the leaf will cool by transpiration in order to maintain its normative temperature (plant 1, Fig. 3). In Fig. 3 we show the plant and air temperatures to be equal under energy limited conditions. This relationship is not universal; the important point is that under energy-limited conditions the temperature of the plant is controlled by the environment and not by the plant.

Sufficient water

Since the thermal control is achieved in large part through transpirational cooling, the availability of water provides a powerful limit on the ability of the plant to maintain its temperature at the T_n. Under conditions where water is limiting, the plant will depart from homeothermic behavior and its temperature will be determined by the environment. The extent to which the temperature of the plant will agree with that of its environment will be dependent on the extent of the water limitation and the timescale over which the water limitation occurs. In our discussions of homeothermy, water availability is assumed to be sufficient to meet all demands.

Humidity

The maintenance of constant leaf temperature that we have proposed is primarily based upon the cooling provided by the evaporation of water from the leaf. The difference in temperature that can exist between an evaporating surface and the air adjacent to it is determined by the amount of water contained in the air. The amount of water in air can be represented by any of several parameters such as vapor pressure deficit, relative humidity, absolute humidity, wet bulb temperature, or dew point temperature. At the dew point temperature, water vapor concentration in the air is at its maximum and any decrease in air temperature will result in the condensation of water vapor. A wet bulb temperature, which is generally higher than the dew point temperature, may be an indicator of the lower limit to which a leaf surface could be cooled by transpiration. The wet bulb temperature, traditionally used as a measure of humidity, is the temperature attained when the air in the boundary layer of a surface is brought adiabatically to saturation by evaporation of water. Like the dew point, wet bulb temperature is dependent upon the amount of water in the air, but unlike the dew point, it is also a function of the air temperature and the geometry of the evaporative surface. Thus the limit on evaporative cooling for a leaf surface is affected by the boundary layer which is a function of wind speed and leaf geometry.

In some environments it is possible that the normative temperature for a plant would be lower than the temperature that can be attained by evaporation. The humidity of the air under such conditions would impose a limit on transpirational cooling that would be above the plant's normative temperature. Thus it would be physically impossible for a plant, even with adequate water, to maintain its temperature at the normative value. Though the plant would be transpiring, the temperature of the leaf would never reach the T_n and the plant would appear to be a "wick" in the sense that both the rate of water use and the temperature of the leaf surface would be entirely controlled by the environment.

An environment in which the humidity limits leaf cooling to a temperature above T_n could be experimentally identified by continuous observations of leaf temperature (plant 2, Fig. 3). When the temperature of the plant is environmentally controlled, its temperature will respond to changes in the environment and leaf temperature will increase with both increasing air temperature and absolute humidity. Below its normative temperature the temperature of the leaf will be controlled by environmental factors (energy limited, plant 2, Fig. 3). When the leaf reaches its normative temperature it will begin to transpire and maintain that value (biological control, plant 2, Fig. 3) in spite of increases in air temperature. At some combination of air temperature and absolute humidity a humidity limitation on cooling can occur and the leaf temperature will respond to changes in the environment (humidity limited, plant 2, Fig. 3).

The hypothesis that the plant is a limited homeotherm suggests that it is possible to experimentally separate high temperature stress from water stress. A plant that is supplied with adequate water and thus under no water stress can be placed in an environment in which the lower limit of evaporative cooling is above the T_n. As previously discussed, under such conditions it is physically impossible for the plant to maintain its normative temperature and thus it will experience a thermal stress in the absence of a water limitation.

CONCLUSION

The interaction between the plant and its environment will perhaps require closer scrutiny in light of the possibility that plants may maintain a stable normative temperature. It is commonly believed that the plant is a passive conduit linking a relatively wet soil with a dry atmosphere.[2,4,5] This proposal of biological control of transpiration by the plant in order to maintain a normative temperature suggests that water use by the plant is not entirely a passive process. If the plant is indeed functioning as a limited homeotherm, its water use cannot be considered as a wasteful process that should be minimized but rather a carefully controlled process for maintaining a temperature conducive to optimal metabolism. Given that the plant actively controls its transpiration, efforts to limit water use may be ill-conceived and may ultimately do more harm than good.

Maintenance of a normative temperature requires that the biology of transpiration be closely coupled with the energetics of the environment. The environment will determine: (1) whether the plant can reach its normative temperature; (2) the amount of water that must be transpired in order for the plant to maintain its normative temperature; and (3) whether the plant can maintain its normative temperature by evaporative cooling. The maintenance of temperature at the normative value will require a high degree of transpirational control and those factors that impact transpiration can be expected to affect the maintenance of the normative temperature by the plant.

Assuming that the plant is a limited homeotherm and thus will transpire in order to maintain a normative temperature, it may be possible to predict the interaction of a particular plant with a given environment. The ability of the plant to reach and maintain its normative temperature within a specific environment will be dependent upon the interactions among the energy balance of the environment (radiation and air temperature), the humidity of the environment and the availability of water within the environment (either as rainfall or irrigation). These three characteristics of a given environment can be monitored and compared with the normative temperatures for various plant species of interest in order to predict to what extent the plant could maintain its normative temperature. Such predictions might be useful in the evaluation of new crop species.

We have herein presented a conceptual framework that accommodates the stenothermal behavior of some plant enzymes with the eurythermal environments in which they must function. We postulate that the plant is a limited homeotherm, as opposed to an obligate poikilotherm, and as such it is capable of maintaining its temperature at a normative value in a variety of environments. The results of a companion paper[13] based upon an experiment with cotton (*Gossypium hirsutum* L.) support our hypothesis of limited homeothermy. Over the course of that experiment we observed the maintanance of a normative temperature by cotton under a variety of environmental conditions. Observation of thermal behavior of other species under the conditions we have identified for homeothermy in plants will be required to determine the validity of our hypothesis of limited homeothermy for plants in general.

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